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IV.

ON THE YOUNG STAGES OF SOME OSSEOUS FISHES.

By Alexander Agassiz.

Presented Oct. 10th, 1877.

I. *Development of the Tail.*

The structure of the tail of bony fishes has been described by Agassiz, Vogt, Owen, Stannius, Heckel, Huxley, Kölliker, and Lotz. The homocercal tails of bony fishes of the present day were contrasted by Agassiz and Vogt, and subsequently by Heckel, with those of the Ganoids, and of other fishes appearing before the Jurassic period, having so-called heterocercal tails; and they attempted to show that the tails of all homocercal fishes pass during their development, through a heterocercal stage. Heckel, Huxley, Kölliker, and Lotz have plainly shown, that, while the external appearance of the tail of bony fishes is homocercal, their real structure is only a modified heterocercal one: so that, as far as we now know, the tail of all fishes is built upon the modifications of the same type; the caudal fin not differing (as I shall show here), in its mode of development from the primitive embryonic fin, from that of the dorsal or anal fins. The theory of Agassiz, that the heterocercal tail of the young of bony fishes passes gradually into a homocercal one, and that the tail of the young of the bony fishes represents an embryonic stage which is permanent in Ganoids, is apparently overthrown by the well-established fact of the heterocercality of the tail of adult bony fishes modified externally so as to assume a homocercal form.

In the following notes, I shall describe the gradual change of the embryonic tail of several species of bony fishes, and call attention to the presence of an embryonic caudal lobe, which has thus far, apparently, escaped the notice of ichthyologists, and which shows remarkably well the identity of growth between the tails of Ganoids and of bony fishes.

As early as 1856, the late Professor Agassiz noticed in Lepidosteus a peculiar fleshy filament (the extension of the vertebral column) above the caudal fin, capable of independent vibratory motion; and compared the young caudal to a second anal, from its position as an appendage of the lower surface of the dorsal column.

This filament still exists in specimens having a length of eight inches. (See fig. 1.) Professor Wilder has lately * followed the transformations of the tail of the Gar-pike, from the time when the tail of the young Lepidosteus is in the stage corresponding to that of Pl. I. fig. 4, of this paper, until the filament has entirely disappeared, and the tail has assumed the rounded outline of the adult. He has also found traces of this filament in very young specimens of Amia, as a slight undulation of the dorsal edge of the caudal at the termination of the supposed notochord.

The stage figured by Wilder agrees very closely to the stage of Pl. I. fig. 10, of this note, and represents — I have not the least doubt, from having traced its gradual disappearance in so many of our bony fishes — the remnant of the fleshy embryonic filament of our bony fishes and of the Ganoids, as was surmised by Wilder.

I have given in Pl. I., quite in detail, the changes gradually taking place in the tail of a Flounder, from the time it leaves the egg until it has nearly assumed the final shape of the adult. On Plate II., I have given figures of a number of young fish tails, of different species, to show how general is the presence of the embryonic caudal fin, even in a comparatively advanced stage of growth. I have also given on the same Plate a figure of a young Lophius (Pl. II. fig. 9), a few days after its hatching from the egg, to show how extensive are the changes our fishes go through before reaching the adult condition; and I hope to give little by little, in papers I am now preparing, the general history of these changes in the principal families of our marine fishes, commencing with the development of the Pleuronectidæ.

In a young Pleuronectes, just hatched from the egg (Pl. I. fig. 1), the caudal end of the chorda is straight. It extends from the anterior arch between the otolites to its posterior extremity, in a line nearly parallel to the dorsal embryonic fin, nearer the dorsal than the ventral side. The embryonic caudal fin is rounded, and nearly symmetrical above and below, the dorsal fold being the narrowest.

In the next stage figured (Pl. I. fig. 2), the caudal extremity of the chorda has become slightly bent upwards, concave towards the ventral side; and then appears the first trace of the division line *f* between the embryonic and the permanent caudal fins; also, traces of the principal caudal rays, and of the accessory rays both of the dorsal and ventral side of the tail. In the following stage, the indentation between the embryonic and the permanent caudal has become deeper, the chorda more arched; the caudal fin-rays are well marked, and the permanent caudal now projects well beyond the general outline of the embryonic fin fold. The delicate lines imitating the fin-rays of the permanent fins, are specially prominent in subsequent stages (Pl. I. figs. 5–9). In the tail of the young of Pl. I. fig. 4, the whole tail is thrown up, and has now assumed the regular heterocercal type; the permanent fin-rays of the caudal being all placed on the lower side of the chorda. There is no trace, as yet, of any ossification of the vertebral column; the anterior and posterior supports of the fin-rays, as well as the supports of the accessory dorsal and ventral rays, are all cartilaginous.

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* Notes on the American Ganoids. Proc. Am. Ass. Adv. Sc., 1876, p. 153, Detroit Meeting.

In the next stages (Pl. I. figs. 5–7), the embryonic caudal has assumed the shape of a large independent lobe; the permanent fin proper extending entirely below it, and forming an independent fin, like a second anal, entirely on the lower surface of the notochord. The resemblance of the tail, at this stage, to the tail of Lepidosteus is so striking that I have here given, for comparison, a figure of the tail of the young Lepidosteus (eight inches in length), from which the late Professor Agassiz described the fleshy filament extending independently above the permanent caudal.

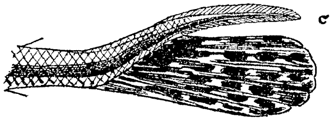

Fig. 1. Tail of young Lepidosteus.

In consequence of the greater arching of the notochord (Pl. I. fig. 5), and the simultaneous growth of the permanent caudal (the embryonic caudal remaining unchanged), the caudal fin is now bilobed. The principal permanent fin-rays of the tail-fin are well developed, but not yet articulated; the dorsal and ventral cartilages of the accessory fin-rays are well separated. In this and the preceding stages, large pigment spots are found between the two principal cartilaginous supports of the fin-rays, and afterwards greatly developed along their outer edge. The large black spot found on the tail of Amia, near the base of the caudal rays, recalls strikingly this space covered by pigment spots. We also find in otner genera (Ctenolabrus), a large pigment spot, remaining more prominent than the others during the whole embryonic growth, and which can still be traced when the young fish has grown to a considerable size. In Ctenolabrus, the large pigment spot is placed on each side at the base of the tail, half-way between the termination of the dorsal and anal fins.

In Plate I. fig. 6, the caudal extremity of the chorda is still more arched upwards, the permanent caudal fin projects as far as the extremity of the embryonic caudal, the lower anterior edge is also separated by a slight indentation from the general line of the primitive embryonic fin-fold, and four or five of the principal caudal rays show a single articulation.

In this and in the subsequent stage (Pl. I. fig. 7), we see the first trace of the gradual disappearance of the embryonic caudal. In Pl. I. fig. 7, the permanent caudal projects beyond the embryonic tail, and there are traces of two articulations in a couple of the principal fin-rays. The permanent caudal has also gradually been thrown more upwards (Pl. I. fig. 8); the fin rays becoming more and more parallel with the axis of the body, until they gradually spread, fan-shaped, on each side (after passing through stage Pl. I. fig. 9) of a central line, as in Pl. I. figs. 10 and 11.

In Pl. I. fig. 8, we have the first sign of the disappearance of the extremity of the notochord, preparatory to the formation of the urostyle. (See Pl. I. figs. 10, 11, and 12.) The permanent caudal is now pointed, projecting far beyond the embryonic caudal, which, in the subsequent stage (Pl. I. fig. 9), is reduced to a slight lobe; it becomes still smaller in the next stage (Pl. I. fig. 10); and is finally reduced to a mere thickened semi-transparent edge, — the last remnant of the original embryonic fin-tail fold to be found in the permanent tail (Pl. I. fig. 11). Accompanying the disappearance of the embryonic caudal, we find a constant increase in the length of the permanent caudal (Pl. I. fig. 9). From being pointed, as in Pl. I. figs. 8, 9, it becomes somewhat rounded; and, with the more symmetrical arrangement of the fin-rays, the edge becomes scalloped as in figs. 10 and 11, and it does not differ materially from that of the adult in its general outline. In fig. 11, we can plainly see the ossification of the vertebræ, with the corresponding apophysis, the urostyle, the two principal cartilages supporting the fin-rays, with the dorsal and ventral cartilages supporting the accessory fin-rays. This is better shown in fig. 12, — a magnified drawing of the base of the tail of fig. 11.

The other genera of bony fishes in which I have traced the presence of this embryonic caudal lobe, or a trace of it, are Atherina, Batrachus, Cottus, Ctenolabrus, Lophius, Gasterosteus, Fundulus, Phycis, Gadus, Menhaden, Temnodon, Labrax, Scomber, six species of Pleuronectidæ, Poronotus, Lumpus, several of the genera of Viviparous fishes (Embiotocoidæ) from San Francisco, and a few other species as yet undetermined. In the very youngest specimens of Syngnathus I have been able to examine (fig. 2), the position of the two supports of the caudal rays, below the upturned termination of the notochord differed in no wise from that of the other bony fishes here mentioned.

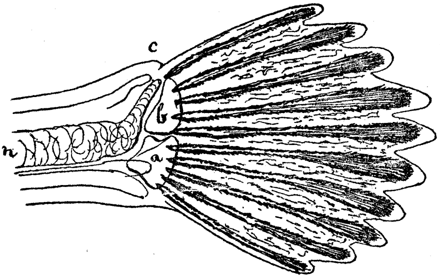

Fig. 2. Tail of young Syngnathus, ¾ in. long.

In Atherina, Pl. II. figs. 1–4, the embryonic caudal does not form quite so marked a lobe as in the species figured in Pl. I. Still, the separation between the permanent and the embryonic caudals is sufficiently well-marked to leave no doubt of the existence of the caudal lobe. The same is the case with Batrachus (Pl. II. fig. 5), with Lumpus (Pl. II. fig. 6), and Ctenolabrus (Pl. II. fig. 7). In the young Poronotus (Pl. II. fig. 8), the embryonic caudal lobe is more prominent.

In Lophius, the termination of the notochord remains unchanged quite late in life; the tail of the young Lophius (Pl. II. fig. 10) showing no trace of any ossification of the vertebral column, or degeneration of the extremity of the notochord, at a time when the young fish can readily be recognized as a young Lophius, from the presence of the peculiar appendages of the pectorals and of the anterior dorsal. In Gasterosteus (Pl. II. fig. 13), the embryonic caudal is again very prominent: it can readily be traced in Pl. II. figs. 14, 15, until the tail has assumed the shape it finally takes in the adult. In all the genera thus far described, the tail gradually passes from a strictly ventral appendage, placed below the dorsal column, to that of a terminal tail placed in the continuation of the vertebral column.

In Phycis and in the Cod, the structure of the tail is somewhat different; the accessory fin-rays, both of the dorsal and ventral side, are very numerous (Pl. II. figs. 19, 20), far outnumbering what are usually called the principal rays of the tail. These accessory rays early make their appearance (Pl. II. fig. 18); so that, although the terminal part of the chorda is turned up as in other fishes (Pl. II. figs. 19, 20), and the two principal cartilages of the tail-fin are placed below it, as in other fishes, yet, owing to this, the separation between the embryonic and permanent caudals is never distinctly indicated (Pl. II. figs. 18, 19, 20) — at least, not in specimens I have had the opportunity of examining — by an indentation or a sharp notch, as in other species figured in this paper. The tail of Phycis and of Gadus, therefore, which at first glance are so beautifully homocercal, do not in reality differ from the tails of other bony fishes; having like them a truly heterocercal termination (Pl. II. fig. 17), but completely disguised by the great development of the accessory fin-rays of the dorsal and ventral sides (Pl. II. figs. 19, 20).

In addition to the similarity of structure of the embryonic tail of bony fishes with that of the Ganoids, we find another point of comparison in the fleshy, fringed pectoral fins, which recall Huxley's Crossopterygians. This fleshy pectoral seems to be quite generally present in the embryos of bony fishes. It is represented for Lophius, on Pl. II. figs. 9, 11, 12. I have found similar fleshy, fringed pectorals in the embryos of Cottus and of several other bony fishes. In fact, immediately before the appearance of the rays in the pectorals, all bony fishes may be said to have such fringed, fleshy pectorals. They are, however, not sufficiently large and prominent to affect the general appearance of the young fish, except in the genera Lophius and Cottus, and one or two others; but in these genera they are well developed, and are similar in structure to the fleshy pectoral of young Lepidosteus.

Carus has called attention, in the Leptocephalidæ,* to the peculiar mode of termination of the chorda, — slightly bent upwards. The filament forming the tail-fin of Tilurus, the forked tail of some of the species of Leptocephalus, and the peculiar ending of their tail, recalling heterocercal tails, are certainly embryonic characters, — judging, at least, from similar stages of many of our common osseous fishes. These characters, with others, — such as the unossified chorda, the transparency of the body, the large prominent pigment spots, — all go far towards confirming the view of Carus, that the Leptocephalidæ are only the embryos of other fishes, such as Cepola and Trichiurus.

Both Huxley and Van Beneden † contend that the facts which they bring forward completely refute the theory of the parallelism of the embryonic tails of bony fishes with those of fishes preceding the Jurassic period: Huxley, because the bony fishes of the present day are not provided with a structurally homocercal tail (as was supposed by Agassiz and Vogt), but have — as he showed from Gasterosteus, and as I have shown here from many other genera of bony fishes — a truly heterocercal structure; Van Beneden, because in the Plagiostomes the tail of the young fish is at first truly homocercal, this condition preceding the heterocercal one, while, according to Agassiz and Vogt's theory, the young Plagiostomes should possess pre-eminently heterocercal tails; and, taking it also for granted that the oldest fossil fish known possessed truly homocercal tails, the whole theory, according to him, falls to the ground.

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* Carus, J. V., Ueber die Leptocephaliden. Leipzig, 1861, p. 13.

† Van Beneden sur le développement de la queue des Poissons Plagiostomes, Bull. Acad. de Belgique, 3me série, xl. No. 3.

Now, while fully admitting, with Huxley, that what Agassiz and Vogt called homocercal, in the modern bony fishes, is only an external delusion, due to a structure of the bones of the tail, which (as I have shown here) is found in a large number of bony fishes of the present day; while also admitting, with Van Beneden, that the young Plagiostomes, which in the adult have a truly heterocercal tail, yet have, in the early stages, a strictly homocercal (structurally also) tail, — yet I think that neither Huxley nor Van Beneden has upset the theory of Agassiz and Vogt; and that, mistaken as they were in the details, the great generalization remains, of the complete accordance between the embryonic growth and the paleontological development: only it must be carried one step farther; and we must, at the same time, give a somewhat different interpretation of the meaning of the heterocercality of the tail, so prevalent among the bony fishes of the present day, from that given to it by Agassiz and Vogt. Let us preface by stating that the heterocercal tail is not the earliest stage; and that neither Von Baer, nor Agassiz and Vogt, stated this, but merely noticed it as one of the early stages in the fish embryo. In fact, as is well known, the earliest stage of the tail in the egg, and immediately after hatching, is nearly symmetrical; the notochord extending in a straight line towards the tail, with the dorsal and ventral embryonic fins forming a rounded tail, the dorsal fin slightly narrower than the ventral. This stage we might call the Leptocardial (Pl. I. fig. 1), — the earliest form of tail assumed by bony as well as other fishes, which precedes that of the heterocercal tail proper (Pl. I. figs. 3, 4).

So that, as far as embryology is concerned, the tail of the Selachians is formed strictly in accordance with the law of development of other bony fishes; and it only remains to be seen how this accords with the paleontological record.

If we examine the tails of the Devonian fishes, — as we know them from the restorations of Agassiz, Hugh Miller, Pander, Heckel, Pictet, Huxley, and others, — we cannot fail to be struck with the exact parallelism of these ancient fishes, as far as the structure of the tail is concerned, with the structure of the successive stages of the tail of the young Flounder, figured on Plate I. of this paper.

We find, among the Devonian fishes, genera with truly leptocardial tails, like those of Pl. I. fig. 1, such as the genera Glyptolæmus, Gyroptichius; also, genera with slightly modified tails (with the least possible tendency to heterocercality), as in figs. 2 and 3, — Holoptichius and Osteolepis; next, such genera as Glyptolepis, where the heterocercal tail is somewhat more marked, approaching nearer the form of Pl. I. fig. 4. But it must be remembered, that in all these genera, although the outline of the tail-fin is much as in the figures here given (Pl. I. figs. 2–4), yet, as in Polypterus and still more in Ceratodus, the scales extended over the dorsal column into the tail, in a triangular shape; and it is only in such genera as Dipterus that the heterocercal character becomes more prominent, as in Pl. I. fig. 4.

This does not by any means conclude the parallelism, which is still more striking when we come to such forms as Phaneropleuron and Tristichopterus, where the tail is lobed, the dorsal column extending into the dorsal lobe exactly as in the stage represented in Pl. I. figs. 5, 6.

In the Old Red, such genera as Acanthodes, Diplacanthus, Cheirolepis, and the like, represent stages corresponding to those of Pl. I. figs. 5, 6, 7, where we find the first indication of the separation of a true caudal and of an embryonic caudal. In the subsequent modifications of the tail of fossil fishes (approaching Lepidosteus), the tendency has been gradually to lessen the upper embryonic caudal lobe, and to give greater prominence to what is to become the caudal proper; although there is not, of course, the difference in structure of the fin-rays of the two sections to separate them, as in bony fishes. It is only when we compare these older forms with such genera as Platysomus, Semionotus, Lepidotus, and finally Pachycormus, that we trace the gradual approach to an externally homocercal tail, much by the same process which we readily follow in the embryo fish through the corresponding changes from Pl. I. fig. 8, to Pl. I. fig. 11. The gradual shortening of the extremity of the chorda dorsalis, until it only extends slightly in advance of the base of the caudal rays, is strictly analogous to the disappearance of the embryonic caudal and the gradual development of the permanent caudal from the lobes of the heterocercal tail of the young fish embryo.

In addition to the parallelism of the embryonic and paleontological development of the tail, we find other embryonic characters in the Old Red fishes. I have already alluded to the old-fashioned structure of the pectorals in the embryo of Lophius and other bony fishes; and would call attention to the innumerable embryonic fin-rays (Pl. I. figs. 5–9) of the embryonic dorsals and ventrals, which recall strikingly the similar numerous rays so characteristic of the fins of the older Ganoids.

So that, while Agassiz and Vogt were undoubtedly mistaken in the details of their explanation and comparison of the homocercal and heterocercal tails, yet the parallelism they attempted to prove, not only exists, but can even be carried out far beyond any thing they conjectured. Their very mistakes regarding the heterocercal structure of what they called a homocercal tail in the bony fishes of the present day being (as I have attempted to show) the best proof of the existence of such a parallelism, and the clearest indication possible of the uniformity of structure of the tails of the fishes of the present day with those of the fishes of the most ancient geological period in which fishes have as yet been found. This parallelism could, however, not be conclusively made out, until it was proved that the extension of the chorda dorsalis into the upper lobe of the heterocercal tail gave us the explanation of the peculiar heterocercal structure still to be traced in the so-called homocercal tails of the bony fishes of the present day, long after the disappearance of the upper caudal lobe, which (as I have shown) exists in bony fishes only during a short embryonic period.

DESCRIPTION OF THE PLATES.

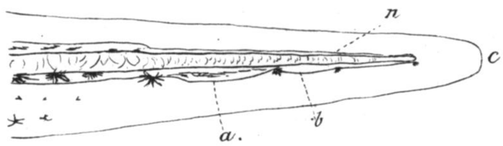
LETTERING.

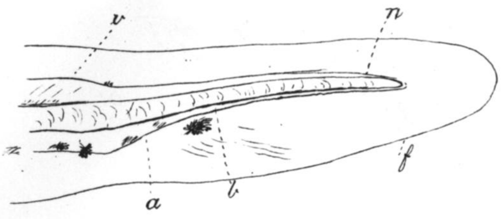
a. Anterior cartilage on lower side of notochord, supporting principal fin-rays.
b. Posterior cartilage on lower side of notochord, supporting principal fin-rays.
a′. Anterior dorsal cartilage.
b′. Posterior dorsal cartilage, supporting accessory fin-rays.
c. Embryonic caudal fin.
d d. Principal caudal rays.
d′. Accessory dorsal caudal rays, above notochord.
d″. Accessory ventral caudal rays, below notochord.
df. Dorsal fin.
vf″. Ventral fin.
f. Permanent caudal fin.
n. Notochord.
v. Last ossified vertebra.
v′. Dorsal apophysis.
v″. Ventral apophysis.
w. Urostyle.

PLATE I.

TAIL OF FLOUNDER.

Fig. 1. Tail of young fish, with straight notochord and embryonic fin.
„ 2. Slightly older — the extremity of notochord somewhat arched, and showing first trace of caudal fin.
„ 3. The indentation between the embryonic caudal and the permanent caudal is deeper; fin-rays well defined.
„ 4. Extremity of notochord still more arched than in preceding figures; the separation between the permanent and embryonic caudals somewhat more distinct.
„ 5. In this stage, the permanent and embryonic caudals form a sharp angle; the distinction between embryonic and permanent rays is well shown.
„ 6. The permanent caudal extends as far as the embryonic caudal, which now shows traces of resorption.
„ 7. The pointed permanent caudal extends beyond the line of the embryonic caudal, somewhat decreased in size.
„ 8. The cartilaginous supports of the fin-rays proper have become large; the extremity of the notochord shows traces of the formation of the urostyle.
„ 9. The permanent caudal has increased greatly in length; the embryonic caudal is now reduced to a small rounded lobe.
„ 10. The caudal has become well rounded; a mere trace of the embryonic caudal is left. The urostyle is also more distinct.





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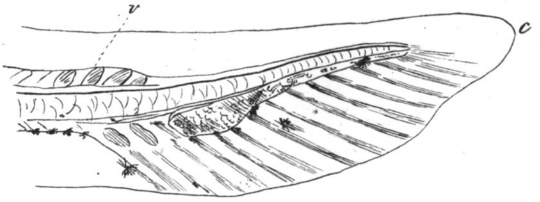

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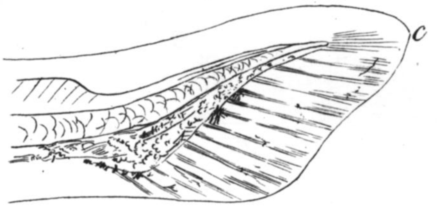

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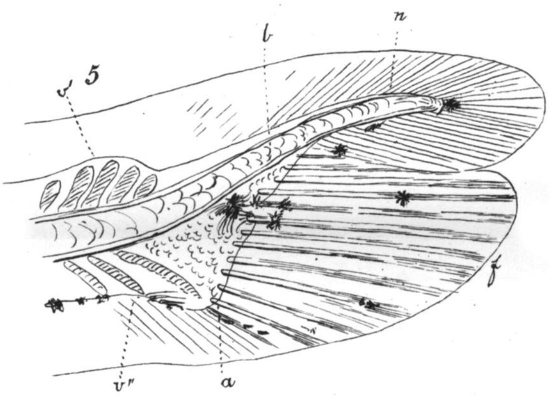

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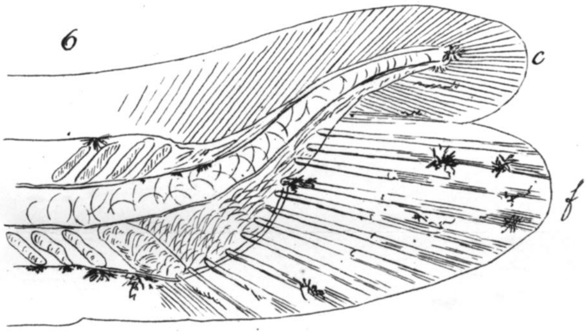

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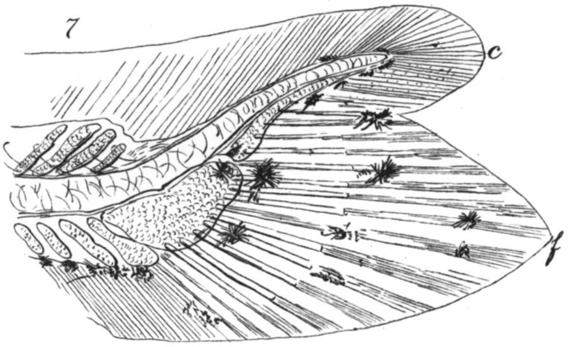

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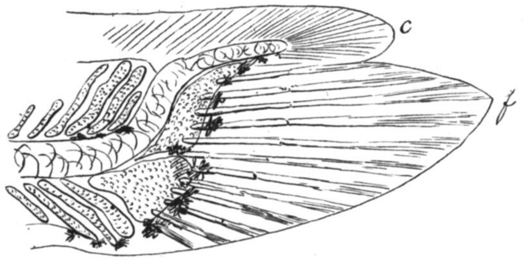

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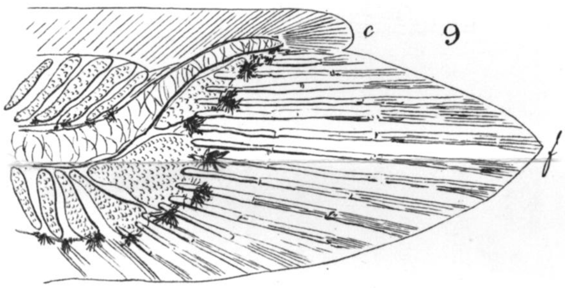

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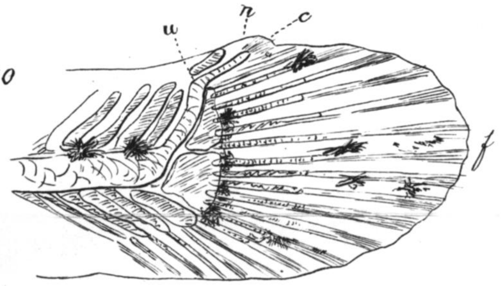

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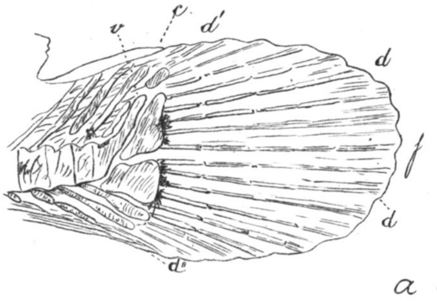

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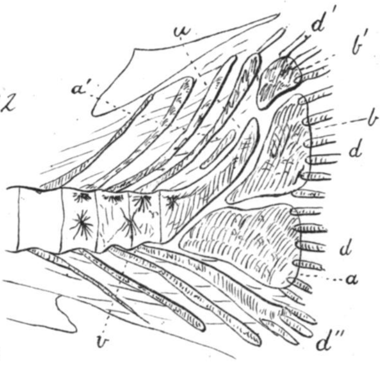

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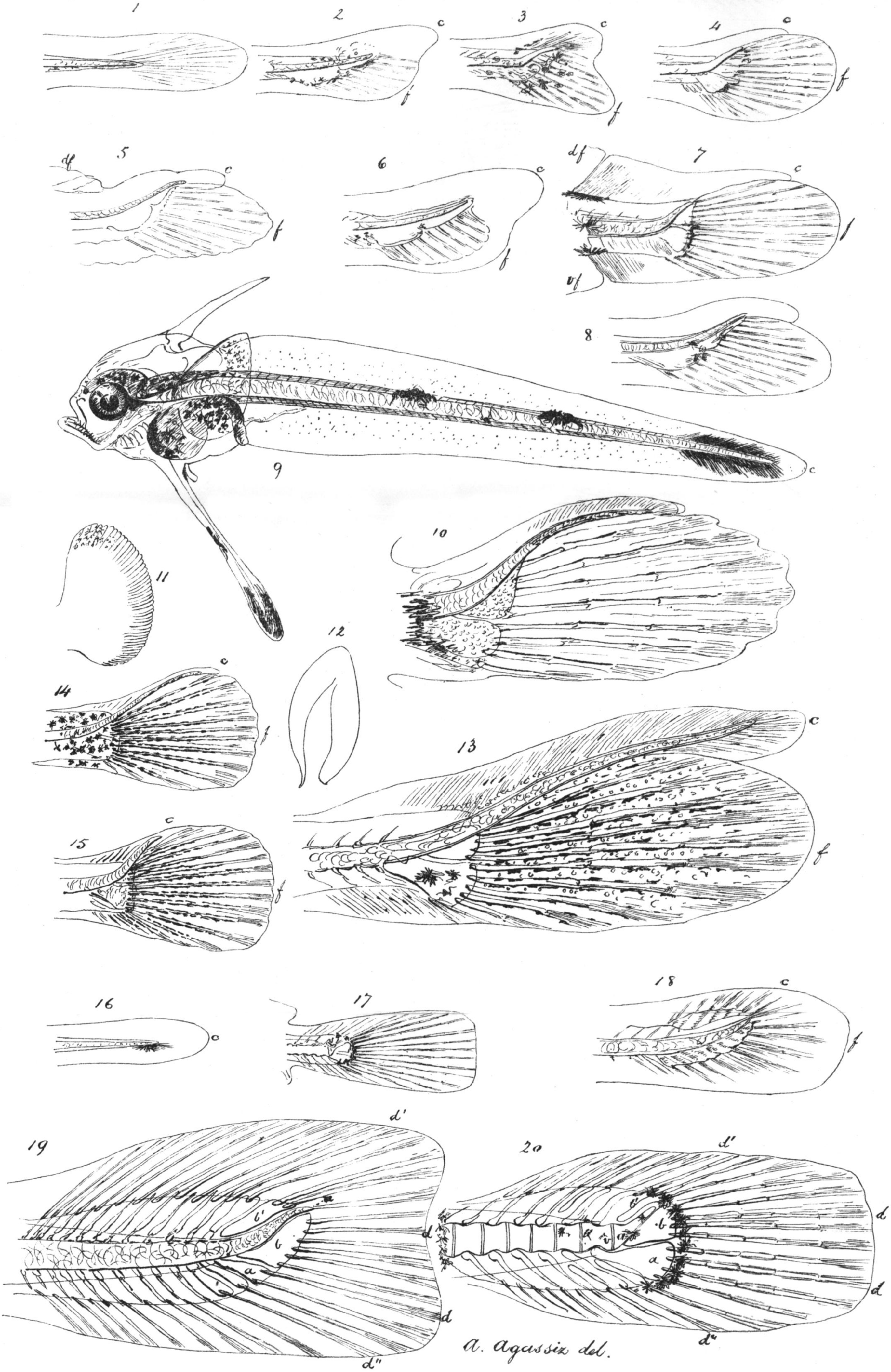

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Fig. 11. The tail has now the shape of that of the adult; the merest trace of the embryonic caudal remains.
„ 12. Fig. 11 somewhat magnified, to show the cartilages supporting the permanent and the accessory fin-rays of the tail, as well as the urostyle with last ossified vetebra.

The young Flounder of Fig. 1 measured $6^{\mathrm{mm.}}$ in length; that of Fig. 12 measured $18^{\mathrm{mm.}}$; the whole change of the tail, from the straight notochord of Fig. 1 to the rounded tail of Fig. 12, took place in about three weeks, judging from the specimens fished up.

PLATE II.

TAILS OF EMBRYOS OF YOUNG FISHES.

Figs. 1–4. Atherina, respectively $5^{\mathrm{mm.}}$, $9^{\mathrm{mm.}}$, $10^{\mathrm{mm.}}$, $11^{\mathrm{mm.}}$ long.
Fig. 5. Batrachus. $9^{\mathrm{mm.}}$ long.
„ 6. Lumpus. $4^{\mathrm{mm.}}$ long
„ 7. Ctenolabrus. $6^{\mathrm{mm.}}$ long.
„ 8. Poronotus. $7^{\mathrm{mm.}}$ long.
„ 9. Young Lophius with straight notochord. About $5^{\mathrm{mm.}}$ long.
„ 10. Heterocercal tail of young Lophius. $20^{\mathrm{m.}}$ long.
„ 11. Fleshy pectoral of same, seen from the side.
„ 12. Same seen from above.
Figs. 13, 14. Gasterosteus.
„ 16, 17, 18. Phycis. Fig. 16 *f.* $3^{\mathrm{mm.}}$, $8^{\mathrm{mm.}}$, $15^{\mathrm{mm.}}$.
Fig. 19. Cod. $20^{\mathrm{mm.}}$ long.
„ 20 and Fig. 18. Magnified. (Phycis.)